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A New Species of *Leptobrachium* from the Kelabit Highland, Northwestern Borneo (Anura, Megophryidae)

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Abstract: Four species of endemic *Leptobrachium* are known from Borneo, two lowland species *L. kanowitense* and *L. abbotti*, a montane species *L. montanum*, and a highland species *L. gunungense*. Of these, both *L. montanum* and *L. abbotti* were found to contain several cryptic species by recent molecular studies. The population from Bario, Kelabit Highland of Sarawak, is one such cryptic species and was once called Lineage 2 of *L. abbotti*. Our morphological survey on this population proved that it has characteristics distinct from all other congeners, and therefore, we describe the Bario population as a new species, *Leptobrachium kantonishikawai* sp. nov. The new species is distinguished from putative topotypes of *L. montanum* and *L. abbotti*, as well as from *L. gunungense* by having a grayish brown abdomen, usually vermiculated, although sometimes spotted or blotched with white, and some unique morphometric characteristics.

Key words: *Leptobrachium abbotti*; *Leptobrachium montanum*; cryptic species; Bario; Borneo.

INTRODUCTION

Six frog species of the megophryid subgenus *Leptobrachium* (sensu Matsui et al., 2010a) of the genus *Leptobrachium* Tschudi, 1838 are currently known from Borneo Island: *L. montanum* Fischer, 1885, *L. abbotti* (Cochran, 1926), *L. gunungense* Malkmus, 1996, *L. hendricksoni* Taylor, 1962, *L. ingeri* Hamidy, Matsui, Nishikawa, and Belabut, 2012, and *L. kanowitense* Hamidy, Matsui, Nishikawa,

and Belabut, 2012 (Frost, 2013). All these species, except for *L. hendricksoni*, whose records on the island require confirmation, and *L. ingeri*, which also occurs on Belitung Island, are endemic to the island (Inger and Stuebing, 1997; Hamidy et al., 2012; Frost, 2013). *Leptobrachium abbotti* and *L. montanum* are distributed widely on the island, chiefly in the lowland forest and in the submontane to montane forest, respectively (Inger et al., 1995; Inger and Stuebing, 1997), whereas *L. gunungense* occurs only on higher altitudes of Mt. Kinabalu (Malkmus, 1996).

Although the lowland species *L. abbotti* is usually distributed in the regions below 1000 m

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a.s.l. in altitude (Inger et al., 1995; Inger and Stuebing, 1997; Malkmus et al., 2002), Zainuddin (1999) recorded the occurrence of this species in Bario, Kelabit Highland of Sarawak at an elevation of more than 1000 m a.s.l., and our survey in Bario from 1991 to 2010 confirmed this finding. Through molecular phylogenetic studies, the population from Bario was found to form a distinct lineage, and was tentatively called *L. abbotti* Lineage 2 (Hamidy et al., 2011). This population is separated from clades of other Bornean *Leptobrachium* by large genetic distances (uncorrected p-distance in 16S rRNA of 5.0–7.2%: Hamidy et al., 2011), whose values are larger than those usually observed among valid species of frogs (Fouquet et al., 2007). In this study, we add morphological data and describe the population from Bario as a new species.

MATERIALS AND METHODS

We first took tissues from muscle and preserved them in 95% ethanol for molecular phylogenetic analyses. Voucher specimens were fixed in 10% formalin, and later transferred to 70% ethanol. For morphological data, we took 21 body measurements following Matsui (1984): 1) snout-vent length (SVL); 2) head length (HL); 3) snout-nostril length (S-NL); 4) nostril-eye distance (N-EL); 5) snout length (SL); 6) eye length (EL, including eyelid); 7) tympanum-eye length (T-EL); 8) tympanum diameter (TD); 9) head width (HW); 10) internarial distance (IND); 11) interorbital distance (IOD); 12) upper eyelid width (UEW); 13) forelimb length (FLL); 14) lower arm and hand length (LAL); 15) outer palmar tubercle length (OPTL); 16) inner palmar tubercle length (IPTL); 17) hand length (HAL); 18) hindlimb length (HLL); 19) tibia length (TL); 20) foot length (FL); and 21) inner metatarsal tubercle length (IMTL). We followed the system proposed by Savage (1975) for the description of toe webbing states. Specimens were deposited in the Graduate School of Human and Environmental Studies, Kyoto University (KUHE) and University Malaysia Sarawak (UNIMAS).

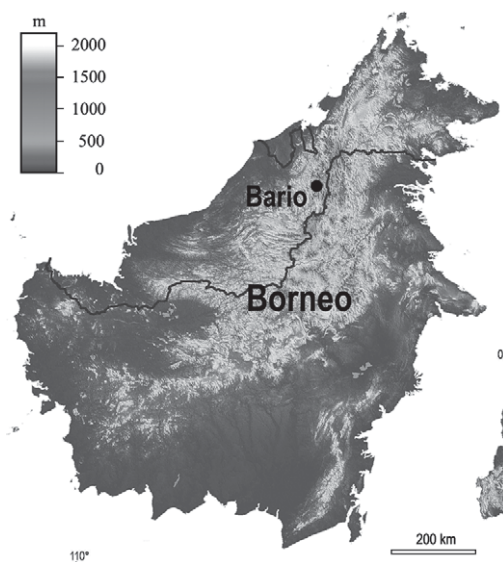


FIG. 1. Map of Borneo, showing the type locality of *Leptobrachium kantonishikawai* sp. nov. (filled circle).

We also studied the holotype of *L. montanum* stored in the Natural History Museum, London (BMNH 86.5.15.10, now 1947.2.25.6).

For the acoustic data, we recorded frog calls in the field using digital recorders (Zoom H2 and Olympus LS-11) at 16 bits and 44.1 kHz as uncompressed wave files, and analyzed them with SoundEdit Pro (MacroMind-Paracomp, Inc.) and Raven Lite 1.0 for Mac OS X (<http://www.birds.cornell.edu/raven>) on a Macintosh computer. Temporal data were obtained from the oscillograms and frequency information was obtained from the audiospectrograms using Fast Fourier Transformation (1024 point Hanning window). Definitions of acoustic parameters follow Matsui (1997) and Dehling and Matsui (2013).

SYSTEMATICS

Leptobrachium kantonishikawai sp. nov.

Figs. 2–4

Leptobrachium abbotti: Zainuddin, 1999, p. 5.

Leptobrachium abbotti Lineage 2 from Bario, Sarawak: Hamidy et al., 2011, p. 37–39.

Leptobrachium montanum: Zainuddin, 1999, p. 5.

Etymology

The specific name is dedicated to Dr. Kanto Nishikawa of Kyoto University, who is a herpetologist active in the Asian region and who assisted us in the collection of the type series.

Holotype

KUHE 53107, an adult male collected on the trail to New Dam, Bario, State of Sarawak, Malaysian Borneo (03°45'N, 115°26'E, 1150 m a.s.l.; Fig. 1) by Kanto Nishikawa and Masafumi Matsui, at 20:00 h on 19 August 2009.

Paratypes

UNIMAS A1/3/0204 (two adults, LBB 0105, 0157) from Lelang, Bario between 1–20 April 1995 by Ramlah Zainuddin; KUHE 53521–53523 adult males, and KUHE 53560, 53562 adult females, all collected from the type locality on 29 August 2010 by Kanto Nishikawa, Koshiro Eto, and Masafumi Matsui.

Referred specimens

KUHE 12225 adult female collected on 11 January 1991, and KUHE 12259 juvenile on 12 January 1991, from Pa Ramapuh, Bario, by Masafumi Matsui; KUHE 12276 adult male collected from Long Lapun between Bario and Gunung (=Mt.) Murud on 16 January 1991 by Masafumi Matsui; KUHE 12381 adult male collected from Pa Belaban, between Bario and Gunung Murud on 25 January 1991 by Masafumi Matsui. KUHE an unnumbered larva from a stream at failed Dam, Bario, on 16 August 2009 by Masafumi Matsui.

Diagnosis

The new species is placed in the genus *Leptobrachium* by having the combination of: femoral gland and axillary gland present; rictal gland and ventrolateral glandular ridges absent; inner palmar tubercle circular, not extending along first metacarpal; vomerine teeth absent; snout and/or dermal palpebral projection absent; spines on upper lip absent

(Matsui, 2013). The new species is also placed in the subgenus *Leptobrachium* from its phylogenetic position (Hamidy et al., 2011). A medium-sized *Leptobrachium*, with adult SVL 43–54 mm in males, and 47–61 mm in females; sclera white; ventrum grayish brown usually vermiculated and sometimes spotted or blotched with white; tympanum visible and usually at least upper one-third dark; laterally brown scattered with black spots from armpit to groin; indistinct black bars on dorsal side of limb; femoral gland large, blotched with white; ova black and white.

Description of Holotype (measurements in mm)

Habitus moderately stocky, body tapering to groin (SVL 54.4; Fig. 2, 3), head broad and depressed, slightly longer (HL 24.7, 45.4% SVL) than wide (HW 23.3, 42.8% SVL); snout rounded from above, truncate in profile, projecting beyond lower jaw; eye large (EL 8.8, 16.2% SVL), obviously projecting from sides of head, slightly smaller than snout (SL 9.8, 18.0% SVL); canthus sharp, lore oblique, moderately concave; nostril lateral below canthus, closer to eye (N-EL 4.9, 9.0% SVL) than to snout (S-NL 5.5, 10.1% SVL); internarial distance (IND 4.5, 8.3% SVL) much shorter than interorbital distance, (IOD 7.2, 13.2% SVL), latter subequal to upper eyelid width (UEW 7.3, 13.4% SVL); pineal spot absent; tympanum weakly visible, diameter (TD 4.6, 8.5% SVL) about half of eye, and separated from eye by about two-thirds of its diameter (T-EL 2.2, 4.0% SVL); no vomerine teeth; tongue heart-shaped, without papillae, notched posteriorly.

Forelimb long and slender (FLL 34.6, 63.6% SVL), about three-fifths of hindlimb; fingers moderately slender, unwebbed; first finger (6.4, 11.8% SVL) slightly longer than fourth and second, third much longer (9.1, 16.7% SVL); blunt, slightly hooked, and not swollen; inner palmar tubercle large (IPTL 2.5, 4.6% SVL), not extending onto first metacarpal and smaller outer palmar tubercle (OPTL 2.1, 3.9% SVL); subarticular tubercles indistinct,

replaced by low callous tissue (Fig. 4A).

Hindlimb slender and relatively short (HLL 64.6, 118.8% SVL); heels not meeting when legs are held at right angles to body; tibia dis-

tinctly longer (TL 19.1, 35.1% SVL) than foot (FL 16.8, 30.9% SVL); tibiotarsal articulation of adpressed limb reaching to middle of tympanum; third toe longer than fifth; toe tips



FIG. 2. An adult male holotype of *Leptobrachium kantonishikawai* sp. nov. (KUHE 53107) in life.

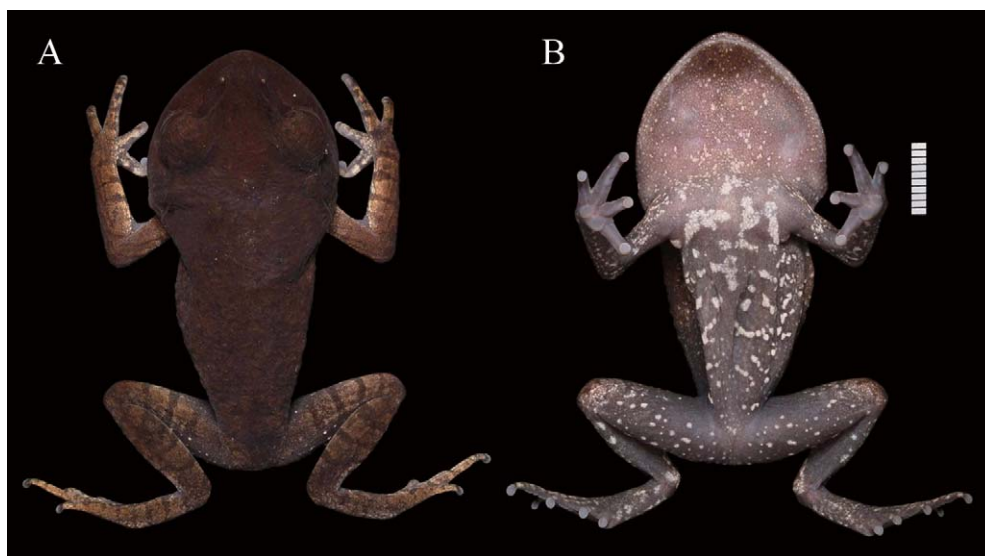


FIG. 3. (A) dorsal and (B) ventral views of a male holotype of *Leptobrachium kantonishikawai* sp. nov. (KUHE 53107) in an anesthetized condition. Scale bar=10 mm.



FIG. 4. Ventral views of (A) hand and (B) foot of the holotype (KUHE 53107) of *Leptobrachium kantonishikawai* sp. nov. (KUHE 53107) in an anesthetized condition. Scale bar=5 mm.

similar to those of fingers; toe webs poorly developed, webbing formula I $1\frac{3}{4}$ –2 II 1–3 III 2–4 IV 4–2 V (Fig. 4B); inner metatarsal tubercle small, low, oval, length (IMTL 2.2, 4.0% SVL) more than half distance between tip of first toe and tubercle (1TOEL 3.7, 6.8% SVL); outer metatarsal tubercle absent; subarticular tubercles replaced by elongate, low callous tissue.

Skin above with reticulate network of thin ridges, minute granules scattered on top of head and dorsum (Fig. 2, 3A); ventrum slightly granular, particularly on belly; a low supratympanic ridge extending from posterior corner of eye to posterolateral region of head; low dermal ridges disposed in longitudinal rows on forelimb and hind limb; a flat pectoral gland at median border of axilla behind arm insertion; right femoral gland small.

Color

In life, head and body dark brown dorsally with very faint darker marking (Fig. 2, 3A); laterally light brown with distinct dots between axilla and groin; iris nearly black; white sclera surrounding iris visible in fully opened eye; upper lip and loreal region without black bars; supratympanic ridge similar to head in color; upper one-third of tympanum darker than

other two-thirds; upper arm uniformly light brown dorsally; lower arm and fingers light brown with distinct black bars dorsally; dorsal part of inner two fingers lighter than outer ones; posterior thigh banded with black bar, continuing to posterior flank; ventrum gray brown vermiculated with white (Fig. 3B); groin and ventral side of hindlimb dotted with white. In preservative, the aspects of the color pattern remain, but the dorsal brown color has darkened.

Variation

Individuals of the type series are generally similar in appearance except for coloration (Fig. 5). Variation in size and body proportions is given in Table 1. No apparent sexual dimorphism is seen, other than that female paratypes have narrower upper eyelid relative to SVL. Tibiotarsal articulation of adpressed limbs reaching to middle of tympanum in the holotype and five paratypes, to posterior edge of tympanum in two, to anterior edge of tympanum in one, and to posterior edge of eye in one. Dark brown dorsal marking is observed in all the paratypes. Smaller paratypes (Fig. 5B) tend to have larger patches of white tubercles on black background of abdomen, giving the impression of abdomen mottled with black and white. However, they have a grayish brown chin like the larger ones (Fig. 5A) and the holotype.

Comparisons

Leptobrachium kantonishikawai sp. nov. differs from some members of the subgenus *Vibrissaphora* [L. (V.) *ailaonicum* (Yang, Chen, and Ma in Yang, Ma, Chen, and Li, 1983); L. (V.) *boringii* (Liu, 1945); L. (V.) *echinata* Dubois and Ohler, 1998; L. (V.) *jiulongshanense* (Wei and Zhao, 1981); L. (V.) *leishanense* (Liu and Hu in Hu, Zhao, and Liu, 1973); L. (V.) *liui liui* (Pope, 1947); and L. (V.) *l. yaoshanensis* (Liu and Hu in Hu, Tian, and Wu, 1978)] by the lack of spines on the upper lip. With a totally black iris, the new species is distinguished from all bicolor-eyed species of the remaining members of the sub-

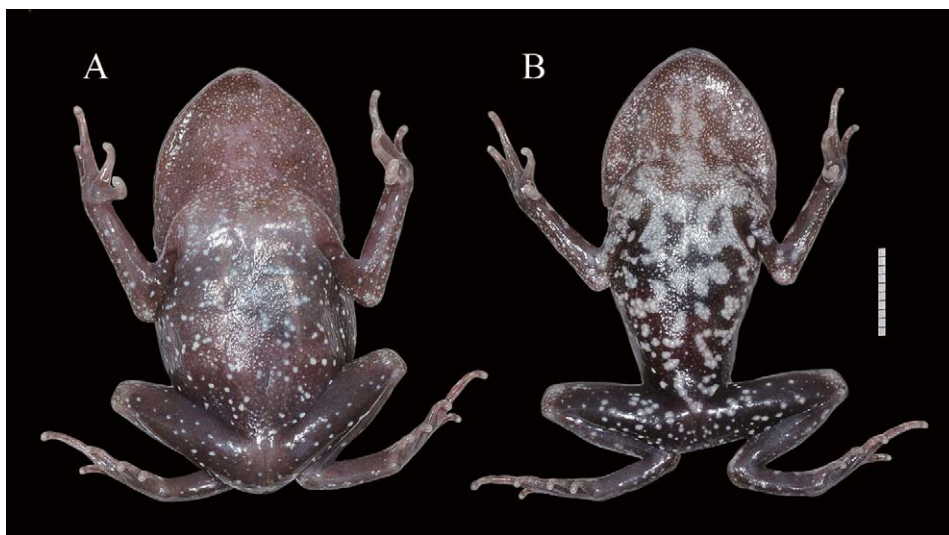


FIG. 5. Variation in the ventral coloration of paratypes of *Leptobrachium kantonishikawai* sp. nov. (A) KUHE 53622 (spotted), (B) KUHE 53523 (blotched). Scale bar=10 mm.

genus *Vibrissaphora* [*L. (V.) banae* Lathrop, Murphy, Orlov, and Ho, 1998; *L. (V.) buchardi* Ohler, Teynié, and David, 2004; *L. (V.) chapaense* (Bourret, 1937); *L. (V.) guangxiense* Fei, Mo, Ye, and Jiang, 2009; *L. (V.) hainanense* Ye and Fei, 1993; *L. (V.) huashen* Fei and Ye, 2005; *L. (V.) leucops* Stuart, Rowley, Tran, Le, Hoang, 2011; *L. (V.) ngoclinhense* (Orlov, 2005); *L. (V.) pullum* (Smith, 1921); *L. (V.) xanthops* Stuart, Phimmachak, Seatun, and Sivongxay, 2012; *L. (V.) xanthospilum* Lathrop, Murphy, Orlov, and Ho, 1998] and the subgenus *Leptobrachium* (*L. hendricksoni*; *L. rakhinensis* Wogan, 2012 and *L. smithi* Matsui, Nabhitabhata, and Panha, 1999). Although the iris color of *L. (V.) masatakasatoi* Matsui, 2013 is unknown, *L. kantonishikawai* differs from it by a dorsoventrally narrower snout and the absence of dorsal dark spots and reticulated flank. Having totally black eyes also differentiates the new species from blue-eyed *L. waysepuntiense* Hamidy and Matsui, 2010 and *L. bompu* Sondhi and Ohler, 2011. With white to pale blue sclera, the new species is distinguished from all the other black-eyed species with different color of sclera (orange: *L. (V.) mouhoti* Stuart, Sok, and Neang, 2006; deep blue: *L.*

lumadorum Brown, Siler, Diesmos, and Alcala, 2010; *L. mangyanorum* Brown, Siler, Diesmos, and Alcala, 2010, *L. tagbanorum* Brown, Siler, Diesmos, and Alcala, 2010). Entirely black eye with white to pale blue sclera is shared with *L. hasseltii* Tschudi, 1838, *L. nigrops*, *L. ingeri*, *L. kanowitense*, *L. montanum*, and so-called *L. abbotti* (no information is available for the single holotype specimen of this species: Cochran, 1926). However *L. kantonishikawai* can be easily distinguished from *L. nigrops*, *L. ingeri*, and *L. kanowitense* by larger body size and unpointed finger tips (SVL>43 mm vs. SVL<41 mm in males and tips of fingers pointed in *L. nigrops*, *L. ingeri*, and *L. kanowitense*). *Leptobrachium kantonishikawai* differs from *L. hasseltii* by the absence or presence of only faint dorsal marking (vs. distinct blotches present on back in *L. hasseltii*). Additionally, the new species has larger HL relative to SVL than *L. hasseltii*.

The remaining three species from Borneo are morphologically similar to each other, and exhibit complicated phylogenetic relationships, with several putative cryptic species including the new species (Matsui et al., 2010a; Hamidy et al., 2011). Hamidy et al. (2011) clarified true *L. montanum* to be their *L. montanum*

TABLE 1. Measurements of adult *Leptobrachium kantonishikawai* sp. nov. and allied species. SVL (mean \pm 1SD, in mm) and medians of ratios (R) of other characters to SVL, followed by ranges in parenthesis. See text for character abbreviations.

	<i>L. kantonishikawai</i>		<i>L. abbotti</i> L1	<i>L. montanum</i>	<i>L. montanum</i> L1		<i>L. gunungense</i>	
	Males (n=5)	Females (n=3)	Males (n=4)	Female holotype	Males (n=2)	Females (n=4)	Males (n=4)	Females (n=4)
SVL	48.7 \pm 5.17 (43.1–54.4)	54.2 \pm 6.68 (47.2–60.5)	62.3 \pm 3.57 (57.4–65.1)	63.0 —	56.8 (56.1–57.4)	60.0 \pm 9.41 (48.6–71.6)	44.0 \pm 5.93 (39.2–52.6)	59.4 \pm 3.46 (55.4–63.8)
RHL	45.4 (44.9–48.5)	46.1 (44.4–46.2)	43.9 (43.1–45.6)	44.8 —	45.2 (44.7–45.6)	44.0 (43.4–44.9)	44.4 (43.2–47.7)	44.2 (43.0–46.5)
RHW	42.8 (41.7–44.5)	43.9 (43.5–44.3)	43.0 (42.4–43.2)	44.0 —	43.2 (42.9–43.5)	41.9 (40.6–43.2)	44.7 (42.7–45.4)	43.3 (37.0–45.3)
RIND	8.3 (7.8–8.8)	8.1 (7.8–9.1)	7.6 (7.3–7.9)	7.0 —	7.8 (7.8–7.8)	7.8 (6.4–8.1)	9.3 (8.9–9.4)	8.6 (8.5–8.9)
RIOD	14.4 (13.2–16.5)	15.0 (14.5–15.3)	13.5 (12.4–14.7)	14.0 —	13.0 (12.4–13.7)	12.8 (11.1–14.4)	14.5 (13.3–16.3)	14.3 (14.1–14.6)
RUEW	13.5 (13.2–15.3)	12.4 (11.9–12.5)	11.5 (11.1–13.2)	9.2 —	11.5 (11.4–11.5)	13.1 (12.7–15.1)	12.6 (11.6–12.8)	11.3 (10.7–11.8)
RSL	19.3 (17.7–20.0)	19.3 (19.1–20.2)	17.7 (16.3–18.5)	— —	17.0 (16.9–17.1)	17.2 (16.2–17.9)	17.6 (16.7–18.6)	17.0 (16.6–17.5)
REL	16.2 (14.8–17.5)	15.6 (14.9–15.7)	13.9 (13.5–16.6)	16.2 —	15.8 (15.7–15.9)	16.0 (15.2–16.6)	14.7 (14.5–15.8)	13.0 (12.8–13.9)
RLAL	55.1 (50.9–58.0)	55.7 (53.8–56.8)	54.9 (50.8–61.6)	53.8 —	55.8 (55.3–56.3)	54.0 (53.5–57.4)	53.3 (50.6–56.4)	55.7 (53.3–57.1)
RFL	68.0 (63.6–74.9)	70.2 (68.5–73.1)	64.7 (58.2–73.9)	74.8 —	70.0 (69.9–70.2)	71.4 (70.6–73.7)	64.4 (61.2–68.9)	67.6 (64.6–73.5)
RTL	35.4 (27.7–39.2)	37.5 (37.3–38.0)	38.2 (37.3–40.2)	37.3 —	39.8 (39.5–40.1)	37.8 (37.3–38.5)	37.5 (35.9–39.5)	38.3 (38.0–39.7)
RFL	34.2 (30.9–36.2)	34.0 (33.3–35.2)	31.0 (29.0–35.5)	34.1 —	34.5 (33.9–35.2)	33.7 (31.7–35.4)	35.2 (32.7–37.8)	35.1 (34.2–36.3)
RHLL	118.8 (113.2–133.4)	123.7 (120.9–125.0)	118.1 (117.6–135.7)	129.0 —	127.7 (125.8–129.6)	127.4 (121.8–130.2)	118.1 (116.2–124.6)	119.8 (115.8–123.3)
RIMTL	4.0 (3.7–5.1)	4.7 (3.6–4.9)	3.3 (2.7–4.4)	2.9 —	3.8 (3.7–3.8)	4.2 (3.8–4.5)	3.6 (3.0–4.3)	3.8 (3.7–4.3)

Lineage 1, and also suggested true *L. abbotti* to be their *L. abbotti* Lineage 1. As noted by them (Hamidy et al., 2011), the holotype of *L. abbotti* is now too badly faded to identify the original color pattern (Inger et al., 1995), but the presence of dark ventral marking is never mentioned in the original description of the species (Cochran, 1926). Samples of *L. abbotti* Lineage 1 were obtained from lowlands of Kutai and Berau, eastern Kalimantan, and Tawau, eastern Sabah. Of these, Kutai is geographically nearest to Balikpapan, the type locality of *L. abbotti*, among samples genetically examined. Thus, Hamidy et al. (2011) tentatively assigned their *L. abbotti* Lineage 1 to true *L. abbotti*, although it is possible that the true *L. abbotti* may represent a different

genetic clade or synonym of *L. montanum* that has no ventral marking.

It is thus pertinent at present to compare the new species with these genetic clades. Although the small sample size does not allow statistical tests, the variation range of some morphometric characters does not overlap between *L. kantonishikawai* and three other Bornean taxa (Table 1). In males, *L. kantonishikawai* has smaller SVL and larger UEW relative to SVL than *L. abbotti* Lineage 1. In this connection, the holotype (male: U. Manthey, personal communication) of *L. abbotti* is reported to be 54 mm in SVL (Cochran, 1926), overlapping *L. kantonishikawai*. Compared with *L. montanum* Lineage 1, *L. kantonishikawai* has smaller SVL and larger UEW and SL, and

smaller TL, all relative to SVL in males, and larger HW, IOD, and SL, and smaller UEW, all relative to SVL in females. *Leptobrachium kantonishikawai* differs from *L. gunungense* by having larger UEW and smaller IND, relative to SVL in males, and larger UEW, SL, and EL, and smaller TL, all relative to SVL in females. Moreover, *L. kantonishikawai* clearly differs from *L. abbotti* Lineage 1 by having grayish brown ground color on the ventral side of head and body (vs. white ventral ground color). The new species has usually distinct white vermiculation on the abdomen, although some have the abdomen spotted with white or mottled with black and white (vs. always heavily mottled with black on abdomen in *L. abbotti* Lineage 1). The holotype of *L. abbotti* is most likely lacking ventral pattern, unlike our *L. abbotti* Lineage 1 or *L. kantonishikawai*, because Cochran (1926) described the undersurface as only yellowish, and never mentioned the presence of ventral marking in her original description. *Leptobrachium montanum* Lineage 1 and *L. gunungense* are similar to *L. kantonishikawai* in having a grayish brown ventral ground color, but at most indistinct marking can be found in some individuals of *L. montanum* Lineage 1.

Range

Known only from around the type locality, Bario, Kelabit Highland, Sarawak, Malaysian Borneo (Fig. 1).

Natural history

A young larva was collected in a small stream ($w < 2$ m) in mid August. Other ecological data are unknown. However, because males were found vigorously calling under fallen leaves in mid to late August, and less actively in late January, the breeding season seems to last for a long time. The trail to New Dam, where the type series was collected is in the secondary forest. Other species found near the trail were: *Ansonia longidigita* Inger, 1960, *Ansonia* sp. 3 of Matsui et al. (2010b), *Phrynoidis juxtaspera* (Inger, 1964), *Leptobrachella mjobergi* Smith, 1925, *Leptolax pictus* Malkmus,

1992, *Limnonectes* cf. *kuhlii* (Tschudi, 1838), *Hylarana picturata* (Boulenger, 1920), *Meristogenys amoropalamus* (Matsui, 1986), *Odorrana hosii* (Boulenger, 1891), *Staurois guttatus* (Günther, 1858), *Staurois tuberlinguis* Boulenger, 1918, *Nyctixalus pictus* (Peters, 1871), *Philautus mjobergi* Smith, 1925, *Polypedates macrotis* (Boulenger, 1891), and *Rhacophorus gauni* (Inger, 1966).

Calls

The following description is based on advertisement calls of the male holotype (KUHE 53107) recorded at an air temperature of 20.8 C. The call is a series of deep squawks, and is delivered intermittently with intercall intervals ranging from 12–35 s ($\text{mean} \pm \text{SD} = 17.7 \pm 8.9$; $n=6$) and a calling rate of 0.049 calls/s (Fig. 6A). A call comprises 3–7 notes (5.4 ± 1.3 ; $n=7$) and call length varies from 2.4 s for three note calls to 3.5 s for seven note calls (Fig. 6B, C). Note duration varies from 200.0–505.0 ms (310.9 ± 78.6 ; $n=39$), and in all calls, the first note is longest ($400\text{--}505$ ms, 452.0 ± 4.0 ; $n=7$) (Fig. 6D) and the last one shortest ($200\text{--}306$ ms, 239.0 ± 37.0 ; $n=7$). Internote interval ranges from 184–712 ms (261.1 ± 134.4 ; $n=32$), and note repetition rate varies from 0.9–1.9 notes/s (1.67 ± 0.34 ; $n=7$). Within a call, relative amplitude is low in the first note, and it steady rises in subsequent notes with apparent peak amplitude achieved by notes at the middle, and then declines towards the end note (Fig. 6C). Amplitude of the first note is approximately half the peak amplitude for the call. Individual notes begin with several distinct pulse groups, followed by a single extended tonal element. In the initial pulse groups, frequency steadily increases from 0.5–0.7 kHz, but remains lower than in the subsequent tonal part, where many harmonics are visible up to 2.3 kHz. Fundamental frequency corresponds to the second (0.7–0.9 kHz) or third (0.9–1.1 kHz) harmonic.

DISCUSSION

Zainuddin (1999) reported that she collected

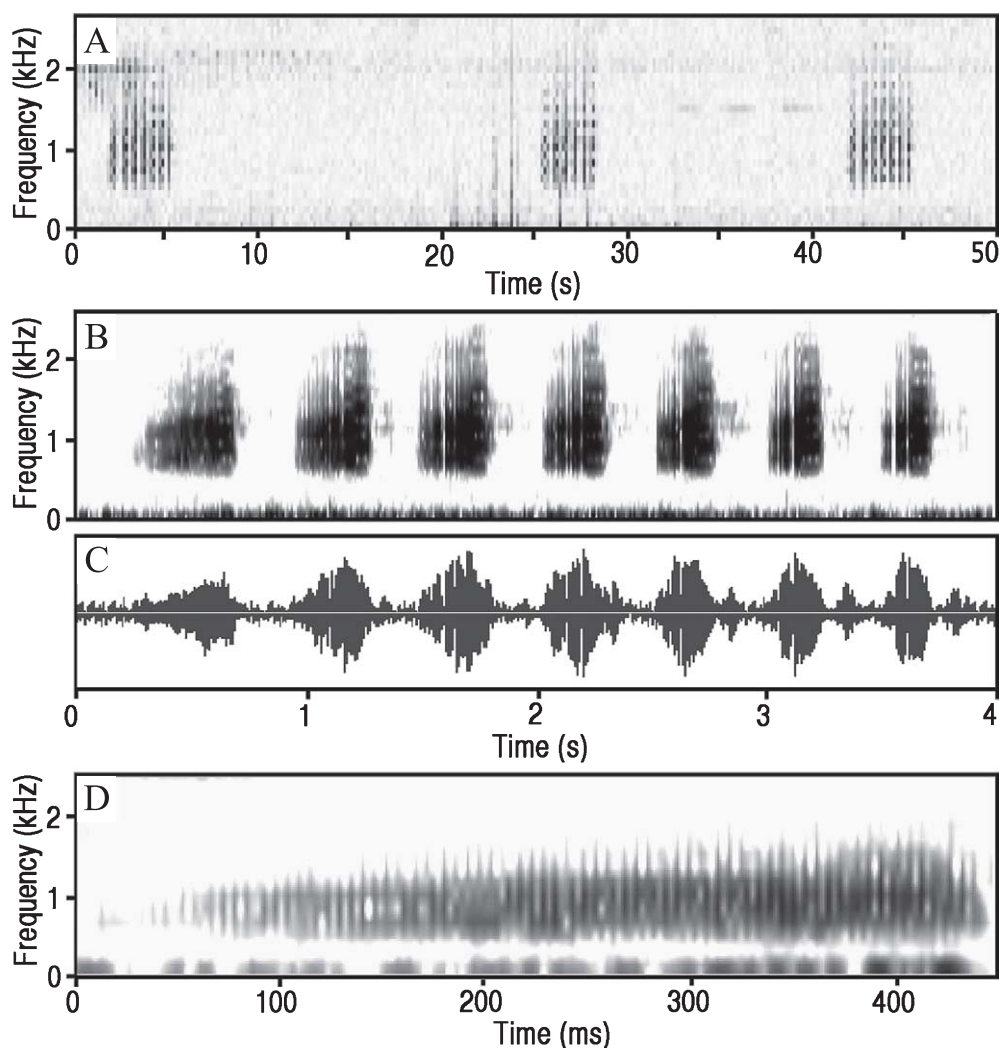


FIG. 6. Spectrograms (A, B, D) and wave form (C) of advertisement calls of the holotype (KUHE 53107) of *Leptobrachium kantonishikawai* sp. nov., recorded at an air temperature of 20.8°C. (A) Three successive calls, (B) seven successive notes (last call in A), and (D) a note (first note in B).

two *L. montanum* at Lelang Baru (=new, auctioneering) Dam Bario, and four *L. abbotti* at Lubang Garam (=salt hole) Pa'Umur. We could briefly examine only two adult specimens, LBB 0105 and 0157, from Lelang, Bario between 1–20 April 1995, which we designated as paratypes of the new species. These two specimens probably correspond to *L. montanum* in Zainuddin (1999). Unfortunately, we could not see *L. abbotti* of Zainuddin (1999), but it would be conspecific with our old specimen of *L.*

kantonishikawai collected from Pa Belaban, a locality further away from Bario and nearer to Gunung Murud than Pa'Umur. As exemplified by this identification problem, some specimens of the new species look like *L. montanum* while others look like *L. abbotti*. This situation would be also the case in other candidate cryptic taxa (Hamidy et al., 2011), and makes the identification of this genus notoriously difficult.

Nevertheless, distribution in the Kelabit

Highland with an elevation near 1200 m a.s.l. (Zainuddin, 1999) is uncommon for *L. abbotti*, which is known to be a lowland species (Inger et al., 1995). Our subsequent molecular analysis showed that the specimens with strong and weak ventral markings are deeply nested in a monophyletic group with very small (<1%) genetic distance in between, and that they form a monophyletic group of the subgenus *Leptobrachium* distinctly separated from other species from Borneo, Sumatra, and the Philippines (Hamidy et al., 2011). Thus, *L. abbotti* continues to be regarded as a lowland species, but the populations now lumped under this name include several cryptic species like *L. kantonishikawai* (Matsui et al., 2010a; Hamidy et al., 2011), and further studies are necessary to solve the taxonomic problems of Bornean *Leptobrachium*.

Zainuddin (1999) recorded 18 anuran species from the Kelabit Highland, but we added many more species in our survey (see above; M. Matsui, unpublished data). The finding of *L. kantonishikawai* together with other recent discoveries of new species such as *Kalophrynus eok* Das and Haas, 2003, *Polypedates chlorophthalmus* Das 2005, *Pelophryne murudensis* Das, 2008, *Pel. linanitensis* Das, 2008, and *Kalophrynus barioensis* Matsui and Nishikawa, 2012, contributed to increasing the number frog species in the Kelabit Highland. These recent discoveries underscore the underestimated diversity of amphibians in this region, which would prove to be a center of frog diversity in Borneo. The discovery of many endemic species in the Kelabit Highland also indicates the necessity of conservation measures in this area.

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APPENDIX 1

Specimens examined

Collection abbreviations are BMNH (Natural History Museum, London), BORN (BORNEENSIS collection, Institute for Tropical Biology and Conservation, University Malaysia Sabah), KUHE (Graduate School of Human and Environmental Studies, Kyoto University), MZB (Museum Zoologicum Bogoriense), SP (Sabah Parks), and UNIMAS (University Malaysia Sarawak).

Leptobrachium kantonishikawai: six males (KUHE 53107, holotype; KUHE 53521–53523, paratypes; KUHE 12276, 12381), three females (KUHE 53560, 53562, paratypes; KUHE 12225), one juvenile (KUHE 12259), and two unsexed adults (UNIMAS A1/3/0204 [LBB 0105, 0157], paratypes) from Bario, Sarawak, Malaysia.

Leptobrachium abbotti Lineage 1: one male (KUHE 44536) from Kutai, East Kalimantan, Indonesia, and three males (BORN 22006–22008) from Tawau, Sabah, Malaysia.

Leptobrachium montanum: one female (BMNH 1947.2.5, holotype) from Parmassan-Alai Gebirge, East Kalimantan, Indonesia.

Leptobrachium montanum Lineage 1: two males (KUHE 42811, 42812) from Paramasan, Banjar, East Kalimantan, Indonesia, two females (MZB Amp 5980, 5981) from Ayi, South Kalimantan, Indonesia, and two females (KUHE 44538, 44539) from Tanah Bumbu, South Kalimantan, Indonesia.

Leptobrachium gunungense: four males (KUHE 39377, SP 26751, 26755, 26760) and four females (SP 26745–26747, 26754) from Mesilau, Mt. Kinabalu, Sabah, Malaysia.

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